NON-RANDOM, SEASONAL OSCILLATIONS IN THE ORIENTATION AND LOCOMOTOR ACTIVITY OF SEA CATFISH (*ARIUS FELIS*) IN A MULTIPLE-CHOICE SITUATION

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ABSTRACT

A quantitative analysis of angular orientation and locomotor activity of 80 sea catfish (*Arius felis*) over 12 consecutive months, under controlled conditions of photoperiod, temperature, and water quality, revealed non-random oscillations in the monthly mean orientation vectors and monthly mean activity of the experimental population. Marquardt modeling of monthly mean activity and of the sine and cosine components of monthly mean orientation indicated significant annual, bimodal cycles for all three variables. These cycles correlated with the observed, seasonal inshore-offshore migrations of *A. felis*, as documented in the literature, and had significant periods of 11.40, 5.11, and 6.64 months for the sine and cosine components of orientation and for activity, respectively. Photoperiod alone apparently acted as the exogenous cue triggering these cyclic changes in orientation and activity.

INTRODUCTION

Seasonal changes in activity patterns have been documented for a number of fishes, *e.g.*, brook trout, *Salvelinus fontinalis* (Eriksson, 1972), the sculpins *Cottus gobio* and *C. poecilopus* (Andreasson, 1973), and burbot, *Lota lota* (Müller, 1973). Brook trout are day-active all year, except for a "desynchronized" interval in summer. The sculpins and burbot are day-active in winter and night-active in summer. Andreasson (1973) suggested that two separate oscillators, one "light-active" and one "dark-active," controlled activity rhythms in these fishes, with seasonal changes in the phase angle between the two proposed oscillators (entrained by exogenous factors) triggering the observed changes in activity patterns. Although these investigators discounted any temperature effect on seasonal activity patterns, Byrne (1968) found that a photoperiod-temperature interaction produced changes in activity patterns of juvenile sockeye salmon, *Oncorhynchus nerka*. In addition, Goodlad *et al.* (1974) demonstrated that, for their study area (four lakes in the Fraser River system), the entrance times of salmon fry into nursery areas were related to seasonal patterns of water temperature (and other factors).

Similarly, the patterns of migration and movements of fishes have been investigated by numerous individuals, several of whom have suggested mechanisms directing the observed behavior. For example, it has been suggested that orientation during migration is associated with various physical, chemical, and biological environmental "clues" (as defined by Harden Jones, 1984a). *e.g.*, direction-resolvable acceleration from ocean swell (Cook, 1984); direction-resolvable Langmuir circulations (Barstow, 1983; Leibovich, 1983); geomagnetism (Quinn, 1982; Walker, 1984); enviroregulation (Neill, 1984); tidal and lunar cycles (Arnold and Cook, 1984;

Pfeiler, 1984); temperature gradients (Dodson and Dohse, 1984; McCleave and Kleckner, in press); and, see the review by Hasler and Scholz (1983).

Beverton and Holt (1957) suggested the theoretical concepts of diffusion and oriented dispersion to explain observed migrations and movements, but these concepts have been applied to very few field results (Saila, 1961). In the Beverton and Holt concept, such "diasporic migration" [a term originally used by Wilkinson (1952) to describe the reassembly of birds dispersed over a large territory back to a breeding zone] is considered satisfactory to explain most examples of fish migration. Beverton and Holt (1957) further postulated that current direction is an orientation clue for migration by marine fishes. Saila (1961) further developed the concept of diasporic migration to explain the annual inshore-offshore migrations of winter flounder, *Pleuronectes americanus.* He did not include a "guiding factor" for direction in this model, and considered the observed "open-water" migration a result of "random search," insofar as fish relocating the coast was concerned. The "homing" phase to specific spawning sites was considered to occur by other means. Saila and Shappy (1963) then formalized this concept of random search into a mathematical model for describing the "open-ocean" phase of salmon migration in returning fish to coastal areas. This random search model (a numerical probability model based on Monte Carlo simulation techniques) was combined with a "low degree" of orientation to an (unspecified) outside stimulus source to produce a "small bias" in the directional orientation of the fish toward their natal coast. The assumptions of the model are oversimplified, and no mechanism for producing the preferred bias in orientation is suggested. However, the random walk model formulated by Saila and Shappy (1963) resulted in a greater return probability of salmon (using only random movement combined with a "small" preferred directional bias) in its simulations than is observed in tag returns. These results indicate that neither the capability for bicoordinate (or, celestial) navigation, nor an extremely precise directional orientation are necessary to insure "successful" migration by fishes. This hypothesis has been supported by Able (1980), Harden Jones (1984a), Leggett (1984), and McCleave and Kleckner (in press).

However, Quinn and Groot (1984a) questioned the correctness of this hypothesis in their criticism of the model formulated by Saila and Shappy (1963). They present convincing evidence that at least three assumptions underlying the model's formulation are incorrect (*i.e.,* salmon swimming speed, duration of migration, and return success). These errors result in a significant under-estimation of the intensity of homeward orientation in migrating salmon. Recent evidence suggests a strong degree of directed orientation in the open-ocean migration of these fishes (Quinn, 1982, 1984; Quinn and Groot, 1984a). Field studies by Hasler *et al.* (1958, 1969) on the open-water orientation and homing of white bass, *Roccus chrysops,* provided earlier support for claims of precise, non-random orientation by fish. White bass were shown to make prolonged, oriented movements in open waters, although the exact mechanism underlying the orientation could not be determined. However, experimental studies on lake-migrating juvenile sockeye salmon have documented mechanisms of solar and magnetic compass orientation in this species (Brannon, 1972; Quinn, 1980; Quinn and Brannon, 1982).

Because a wide variety of animals display compass orientation or directional preferences in artificial testing arenas (Matis *et al.,* 1974; Quinn and Groot, 1984b), it is possible to investigate the mechanisms triggering (*i.e.,* "cues," as defined by Harden Jones, 1984a) and directing (*i.e.,* clues) biases in orientation of some species in the laboratory. For example, Hasler *et al.* (1958) conducted laboratory studies which demonstrated a sun-compass mechanism of orientation in white bass, bluegill

sunfish (*Lepomis macrochirus*), and pumpkinseed sunfish (*L. gibbosus*). Fish were first trained to take food or find shelter in a specific compass direction, using the sun as the only reference clue. Subsequent testing, at a different time of day, showed that the fish were able to compensate for the sun's movement, and orient in the trained direction.

Quantitative investigations of non-random changes in angular orientation of fish have been conducted with goldfish, *Carassius auratus*, by Matis *et al.* (1974, 1977). Their analyses of the monthly mean orientation vectors of 129 fish over a 41-month period (not entirely consecutive) revealed both long-term (monthly) and short-term (hourly) non-random oscillatory changes in the angular orientation of these fish. In addition, the population exhibited a significant long-term cycle (33.6 months) in the sine component of their orientation. However, these authors were unable to relate their findings to natural populations and attempts to provide a mechanism for cueing the observed "seasonal" changes in orientation were inconclusive. Although Matis *et al.* (1974) conjectured that periods of inactivity in the goldfish were related to oscillations in orientation, no quantitative analysis was attempted.

The present study was undertaken to examine quantitatively seasonal changes in both angular orientation and activity in a migratory species. The hardhead sea catfish, *Arius felis*, was selected as the experimental species for several reasons. Firstly, it has been utilized extensively in this laboratory as a bioassay model for examining the behavioral toxicology of copper to marine fishes (*e.g.*, Scarfe *et al.*, 1982; Steele, 1983). All such experiments consist of a control recording of the locomotion of a single, naive sea catfish for 24 h following their placement into a behavioral testing arena in which the locomotion was monitored prior to experimental manipulation with copper. Fish size, treatment prior to monitoring, and experimental conditions during monitoring were identical for all control periods of experiments covering a span of 12 consecutive months. Thus, the data, stored on computer disks, are suitable for a quantitative analysis of seasonal changes in orientation and activity of these fish.

Secondly, sea catfish are dark-active (nocturnal) year-round, although light-to-dark transitions apparently synchronize their diel activity patterns (Steele, 1984, 1985). Thus, a consideration of seasonal changes in diel activity as noted for brook trout (*S. fontinalis*), sculpins (*C. gobio* and *C. poecilopus*), and burbot (*L. lota*) is unnecessary (see Eriksson, 1972; Andreasson, 1973; Müller, 1973). Although photoperiod does produce short-term alterations in orientation patterns in sea catfish, the minimum day-length needed to trigger these alterations in angular orientation (19.2 h) is not considered to be frequently encountered in the fish's natural habitats, and certainly not along the Texas coast (Steele, 1984).

Finally, the natural history of *A. felis* is well-documented (*e.g.*, Henshall, 1895; Hubbs, 1936; Lee, 1937; Gunter, 1947; Ward, 1957) which facilitates relating observed changes in seasonal activity and orientation in the laboratory to the behavior of natural populations. Generally, sea catfish decrease in abundance in the bays and estuaries along the northern coast of the Gulf of Mexico during winter, except in southern Florida, and move to deeper waters offshore or to deep-water "holes" within an estuary system (Gunter, 1947; Gunter and Hall, 1965). This annual offshore migration occurs from approximately October through December in the Northern Gulf of Mexico, along the Texas coast (*e.g.*, Gunter, 1947; Ward, 1957; pers. obs.). According to Franks *et al.* (1972) this species becomes widely scattered during winter months after returning to the Gulf. Although present in small numbers year-round within estuary systems, sea catfish become quite "rare" over winter, but regain abundance during spring and summer as fish return to the

estuaries to spawn (Gunter, 1947; Ward, 1957; Franks *et al.,* 1972; Morgan, 1974; pers. obs.). Although fish begin returning to the estuaries as early as March (Gunter, 1947; Ward, 1957), the spawning season of sea catfish along the northern Gulf coast usually occurs from about the first week in May to as late as the first week in August (Ward, 1957). Observed changes in activity and angular orientation in the laboratory may be correlated with these observed annual inshore-offshore migrations and spawning periods of sea catfish.

MATERIALS AND METHODS

Experimental procedure

Eighty hardhead sea catfish, *Arius felis* (average total length 274 ± 13 mm), were obtained either by hook and line or from a commercial supplier in Port Aransas, Texas, between July and September 1977. They were maintained for at least three months prior to experimentation in slate holding tanks containing filtered, recirculating artificial sea water (30‰ *S;* 21–24°C) and fed every third day with fresh-frozen shrimp, except during behavioral monitoring.

Fish were monitored individually for 24 h, each, in the behavioral monitoring system. All monitoring was conducted in constant darkness to reduce visual clues in the behavioral arena. The monitoring system used for data collection has been described previously in detail (Kleerekoper, 1977). Briefly, it consists of a cylindrical steel rosette tank (210 cm diameter) with double walls forming a peripheral channel. The periphery of the interior is incompletely partitioned into 16 radial compartments and an open central area (110 cm diameter) by hollow wooden dividers. The system operates on the principle of multiple choice in which there is equal access to every compartment. Alternate dividers contain either light sources (705 ± 35 nm) or photodiode arrays, which together form photoelectric "gates" at the entrance to each compartment. Data are collected during an experiment when a fish, on entering or leaving a compartment, activates the photoelectric gate. This "event" is then recorded (as time and compartment identity) via a logic interface onto a high-speed paper-tape punch. Locomotor activity is then quantified on a computer by the total number of events per experiment.

Additionally, the orientation vector (turning angle) of each successive movement between compartments, defined as the angle between the compartments of origin and of destination, is also determined. Each compartment covers an arc of 22.5°, therefore orientation vectors range from 22.5° to 360° at 22.5° intervals, with 180° indicating a straight path across the monitor tank and 360° indicating a return to the compartment immediately vacated. Computer analysis thus produces a time series of absolute orientation vectors of a fish's movements.

Treatment of data

For each fish a frequency distribution of the orientation vectors over an entire 24-h monitoring period was constructed. Since angular resolution is limited to 22.5° intervals, due to tank design, orientation vectors were grouped into 22.5° categories. Table I lists such data for a representative fish.

Prior to analytical modeling of the monthly time series of orientation vectors, it must first be determined whether the series is non-random(*i.e.,* oscillatory). The determination of non-randomness is of prime importance here. Data was first analyzed for each fish to determine the monthly mean orientation vector ($\bar{\theta}$) and the intensity of this mean vector (r_v). Individual data was then pooled for all fish

Frequency distribution of orientation angles for a representative sea catfish, Arius felis *(Expt. No. 938, June 1978)**

Interval midpoint	Frequency	Interval midpoint	Frequency
0 (360)°	88	180°	633
22.5°	84	202.5°	699
45.0°	134	225.0°	516
67.5°	157	247.5°	506
90.0°	133	270.0°	286
112.5°	145	292.5°	131
135.0°	271	315.0°	124
157.5°	351	337.5°	49

* Mean vector: $\bar{\theta}$ = 201°27'; Vector intensity: r_v = 0.4753.

monitored in the same month, and a group monthly mean $\bar{\theta}$ and r_v were calculated. Because orientation data is circular in nature, simple arithmetic means could not be used to determine monthly mean vectors. Analyses were conducted according to the procedures of Batschelet (1965, 1972, 1978, 1981) for handling orientation data. Monthly mean vectors were calculated using the equation,

$$\bar{\theta} = \tan^{-1}(\bar{Y}/\bar{X}) \tag{1}$$

where $\bar{X}$ and $\bar{Y}$ are the set of mean rectangular coordinates of orientation for a data set. These are also termed the (weighted) sines and cosines since,

$$\bar{X} = r \cos \theta \tag{2}$$

and,

$$\bar{Y} = r \sin \theta \tag{3}$$

Operationally, $\bar{X}$ and $\bar{Y}$ are determined using equations (4) and (5),

$$\bar{X} = (\sum w_i x_i)/\sum w_i \tag{4}$$

$$\bar{Y} = (\sum w_i y_i)/\sum w_i \tag{5}$$

where x_i and y_i are the cosines and sines, respectively, of each orientation vector category. The "weights" for each sine and cosine, w_i, are simply the frequency of occurrence of each orientation vector category within a data set (see Table I). The intensity (r_v) of each monthly mean vector was then calculated using,

$$r_v = (\bar{X}^2 + \bar{Y}^2)^{1/2} \tag{6}$$

Second-order statistical analysis of the directional data thus determined for each fish was performed using Hotelling's one-sample test (Hotelling, 1931), as detailed by Batschelet (1978). Rejection of the null hypothesis indicates a concentration of the individual vectors around a mean direction (vector). In this instance, Hotelling's test was performed on each monthly set of individual orientation vectors. Calculation of each monthly test statistic ($F_{2,n-2}$) was performed without the use of a confidence ellipse (see Batschelet, 1978).

Two tests have been found to be statistically powerful for detecting non-randomness in orientation data (Matis *et al.*, 1974) and will be described. The Spearman rank correlation test (Siegel, 1956; Mendenhall, 1975) determines a rank correlation between time (*i.e.*, the month) and the magnitude of the $\bar{X}$ and $\bar{Y}$

components of each monthly mean orientation vector ($\bar{\theta}$). The null hypothesis proposes that time and magnitude are linearly uncorrelated, while the alternative hypothesis indicates either an increasing or decreasing linear correlation. The correlation coefficient, r_s, of a series is determined and its significance tested by exact theory.

Randomness in a series is tested by the Wald and Wolfowitz serial correlation test (Wald and Wolfowitz, 1943). The serial correlation coefficient of lag 1, R_1, measures dependency between consecutive observations and is tested for significance by approximate theory. The null hypothesis states that successive observations are independent. The alternative hypothesis indicates regularity (predictability) in observed fluctuations in the data. These same two statistical tests were also used to search for non-randomness in the monthly mean activity of all fish monitored in a given month.

Together, the Spearman rank correlation test and the Wald and Wolfowitz serial correlation test classify a time series as follows. If the Spearman rank correlation test does not reject the null hypothesis, the significance or non-significance of the serial correlation test indicates either oscillation or random fluctuations in the data, respectively. If, however, linear correlation is indicated, the strength of this correlation is indicated by the serial correlation test (H_0: weak linear correlation). Figure 1 is a decision-making flow chart which summarizes the above procedures.

If oscillation was found in a data set, the $\bar{X}$ and $\bar{Y}$ components (the rectangular coordinates) of each monthly mean orientation vector were plotted for each fish for each month. Both the $\bar{X}$ and $\bar{Y}$ components were then analyzed for periodicity over time according to the cyclical models,

$$\bar{Y}_t = a_1 + A_1 \cos(c_1 t + \Omega_1) \tag{7}$$

$$\bar{X}_t = a_2 + A_2 \cos(c_2 t + \Omega_2) \tag{8}$$

where t is time (in months) and the parameters a_i, A_i, c_i and Ω_i represent the mean level, the semi-amplitude, the frequency and the phase angle parameters, respectively (Bliss, 1970; Matis et al., 1977). A similar model was derived to analyze monthly mean activity and is given by,
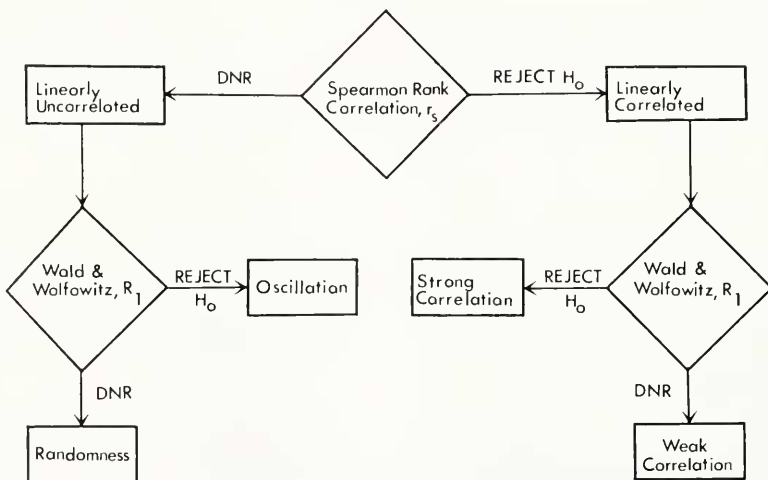

FIGURE 1. Decision-making flow chart used in determining if non-randomness exists in the data. See text for discussion of the statistical tests.

$$\bar{Y}_{act} = a_3 + A_3 \cos{(c_3 t + \Omega_3)} \tag{9}$$

where $\bar{Y}_{act}$ is used as conventional regression notation and does not indicate a component of rectangular coordinates.

These models were fitted to the data by the Marquardt technique of nonlinear least squares (Marquardt, 1963; and see Draper and Smith, 1981; Matis *et al.*, 1977), which generates combinations of the parameters (a_i, A_i, c_i and Ω_i) to minimize the error sum of squares (SSE). Although the theory of nonlinear least squares does not guarantee that a given set of parameters which produces the smallest local minima on the SSE hypersurface represents the absolute minimum of the SSE, those parameter sets which do will be considered the "best-fitting" cycle for each model, respectively.

RESULTS

The monthly mean orientation vectors ($\bar{\theta}$) and their intensities (r_v) are given in Table II and illustrated in Figure 2 (which also contains the individual data). The

TABLE II

Composite monthly mean vector, vector intensity, and monthly mean activity for sea catfish, Arius felis

Month[a]	Monthly code (m)	N	Total no. observations in mean vector	Total no. hours of recording	Angle ($\bar{\theta}$) of mean vector	Intensity (r_v) of mean vector	Monthly mean activity[b] ($\pm$S.D.)
Jan	0	6	28,688	144	189°57'	0.4222	4778 (648.55)
Feb	1	7	45,269	168	195°55'	0.3346	6467 (753.91)
Mar	2	7	52,080	168	266°22'	0.2952	7440 (749.43)
Apr	3	6	37,590	144	257°05'	0.0709	6265 (531.77)
May	4	6	29,544	144	215°15'	0.0580	4924 (708.15)
June	5	8	33,440	192	181°10'	0.3387	4180 (567.65)
July	6	6	26,268	144	149°25'	0.0284	4378 (636.82)
Aug	7	6	34,392	144	119°14'	0.2302	5732 (766.14)
Sep	8	7	56,679	168	94°22'	0.1837	8097 (1713.91)
Oct	9	8	57,344	192	88°14'	0.1996	7168 (694.95)
Nov	10	6	39,882	144	179°49'	0.3229	6647 (850.51)
Dec	11	7	35,021	168	183°55'	0.3304	5003 (772.91)

[a] All months in 1978.
[b] Activity quantified as the number of entries into compartments in the behavioral monitoring arena per 24 h.
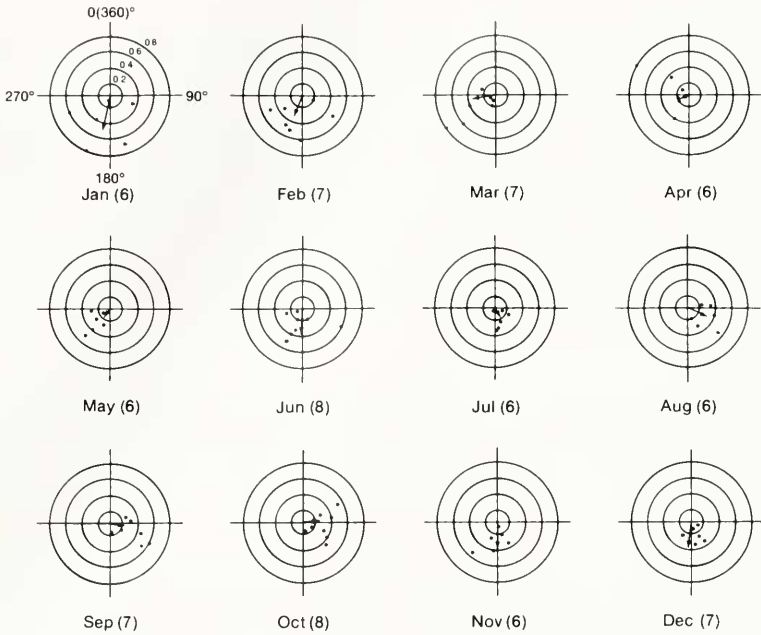
FIGURE 2.   Monthly mean orientation vectors from January 1978 to December 1978 for 80 sea catfish (*Arius felis*). Number of fish in parentheses; vectors of individual fish are plotted in each month.

weighted sines ($\bar{Y}_t$) and cosines ($\bar{X}_t$) of the monthly mean vectors are plotted in Figures 3 and 4, respectively. Monthly mean activities are also listed in Table II and are plotted in Figure 5. Table III contains the results of Hotelling's test on the individual orientation data for each month. The individual vectors are significantly concentrated around the monthly mean vector for each month except January.
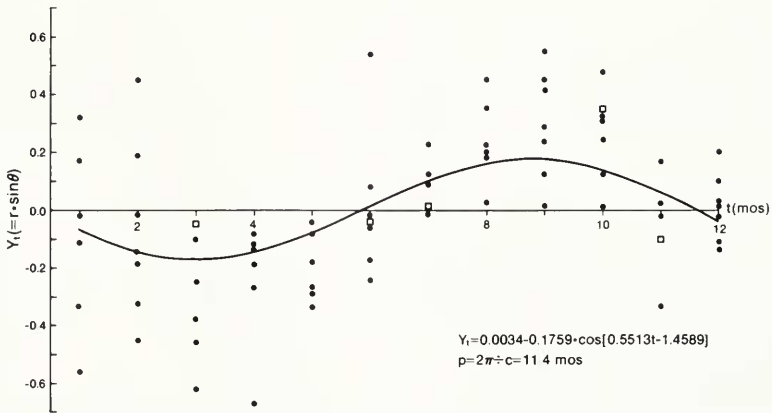

$$Y_t = 0.0034 - 0.1759 \cdot \cos[0.5513t - 1.4589]$$
$$p = 2\pi \div c = 11.4 \text{ mos}$$

FIGURE 3.   Observed and fitted values of sine, Y_t, of monthly mean orientation vectors for 80 sea catfish (*Arius felis*) plotted against month, t, of observation. Parameters of the cyclical model used to fit the data (mean level, semi-amplitude, frequency, and phase angle, respectively) and period of oscillation are also given. Open squares indicate more than one data point.
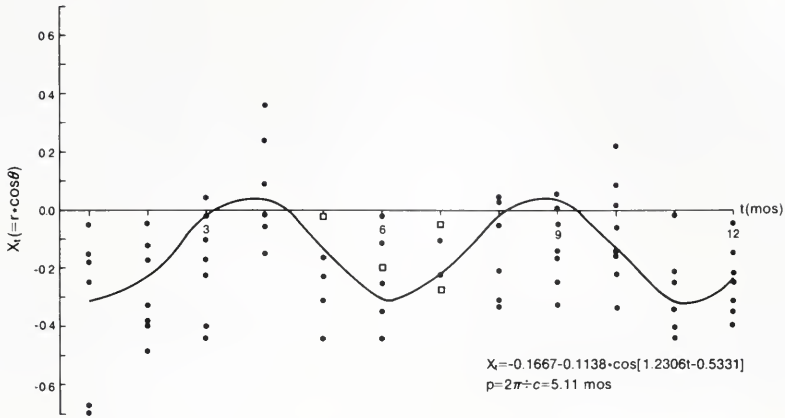
FIGURE 4.   Observed and fitted values of cosine, X_t, of monthly mean orientation vectors for 80 sea catfish (*Arius felis*) plotted against month, t, of observation. Parameters of the cyclical model used to fit the data (mean level, semi-amplitude, frequency, and phase angle, respectively) and period of oscillation are also given. Open squares indicate more than one data point.

The apparent tendency of the monthly mean vectors of sea catfish to oscillate non-randomly with time (Fig. 2) was confirmed by the results of the Spearman rank correlation and the Wald and Wolfowitz serial correlation tests performed on the rectangular coordinates (*i.e.*, the weighted sines and cosines) of the vectors. Neither the time series of sines ($r_s = -0.478$) nor cosines ($r_s = 0.098$) reject the null hypothesis, indicating nonlinearity in the data ($r_{s12,0.05} = \pm 0.591$). The subsequent serial correlation tests indicate significant oscillation ($R_{I12,0.01} = \pm 0.780$), with $R_I = 0.865$ and $R_I = 0.830$ for $\bar{Y}_1$ and $\bar{X}_1$, respectively. Similar statistical results confirm non-random oscillation in the observed monthly mean activity of the fish with $r_s = 0.196$ and $R_I = 0.889$.

Table IV lists certain parameter combinations which yield minimal SSE for the cyclical models of the $\bar{Y}_1$ and $\bar{X}_1$ components of the monthly mean orientation vectors and for the cyclical model of monthly mean activity of sea catfish. Although
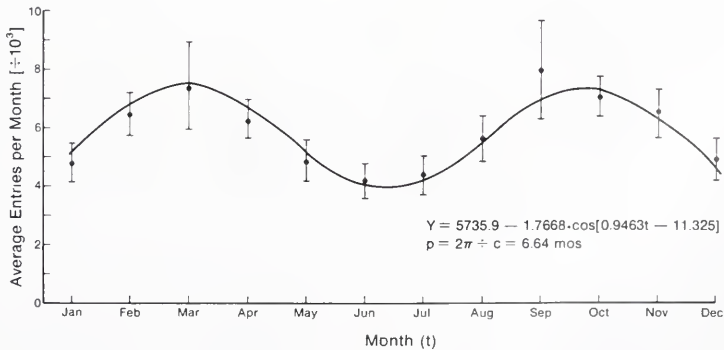

FIGURE 5.   Observed and fitted values of monthly mean activity, Y_{act}, of 80 sea catfish (*Arius felis*) plotted against month of observation, t. Parameters of the cyclical model used to fit the data (mean level, semi-amplitude, frequency, and phase angle, respectively) and period of oscillation are also given. Numbers of fish observed each month are given in Table II.

TABLE III

Results of Hotelling's second-order test on the individual orientation vectors per month for sea catfish, Arius felis

Month	N	$F_{2,n-2}$	Month	N	$F_{2,n-2}$
Jan	6	3.12[NS]	July	6	12.27[a]
Feb	7	9.01[a]	Aug	6	7.92[a]
Mar	7	5.94[a]	Sep	7	9.39[a]
Apr	6	6.95[a]	Oct	8	10.52[a]
May	6	7.21[a]	Nov	6	7.83[a]
June	8	10.70[a]	Dec	7	15.08[b]

NS = Not Significant; [a]$P \leq 0.05$; [b]$P \leq 0.01$. See Mendenhall (1975) for critical F-values for each value of $F_{2,n-2}$ (or any comparable statistics text).

three sets of parameters are listed for each model for comparison, following the decision criteria described, the parameter sets producing the smallest residual SSE for each model were designated "best-fitting," and are the only ones plotted in Figures 3–5 and further discussed. The total (corrected) sums of squares for $\bar{Y}_t$, $\bar{X}_t$, and $\bar{Y}_{act}$ are 5.70599, 2.84663, and 4.18387, respectively. Thus, the "best" model for $\bar{Y}_t$ (frequency = 0.5513) is significant ($P \leq 0.001$) with $F_{4,76} = 14.98$; that for $\bar{X}_t$ (frequency = 1.2306) is also highly significant ($P \leq 0.001$) with $F_{4,76} = 26.04$;

TABLE IV

Parameter combinations (± asymptotic standard error for the "best-fitting" model) yielding local minima on the SSE hypersurface

A. Sine component of orientation, Y_t

a_1	A_1	c_1	Ω_1	SSE	F-value[a]
0.00340	−0.17588	0.55132	−1.14589	3.19402	14.98
(±0.02170)	(±0.03130)	(±0.04690)	(±0.32594)		
−0.00261	−0.15026	0.54390	−1.02940	3.53778	
−0.02176	−0.09426	0.43086	−0.37075	4.20367	

B. Cosine component of orientation, X_t

a_2	A_2	c_2	Ω_2	SSE	F-value[a]
−0.16673	−0.11378	1.23058	−0.53312	2.31088	26.04
(±0.02023)	(±0.02745)	(±0.08022)	(±0.50694)		
−0.16362	−0.11076	1.27339	−0.84907	2.33175	
−0.16891	−0.10535	1.17558	−0.13387	2.33984	

C. Activity, Y_{act}

a_3	A_3	c_3	Ω_3	SSE	F-value[b]
5.73587	−1.76680	0.94632	−11.32450	1.75769	4.97
(±0.14791)	(±0.20497)	(±0.03027)	(±0.19310)		
5.74040	−1.70508	0.94323	−11.33090	1.79394	
5.73078	−1.61667	0.98327	−11.30412	3.03329	

[a] Significant at $P \leq 0.001$; [b]significant at $P \leq 0.005$.

and, the "best" model for $\bar{Y}_{act}$ (frequency = 0.9463) is highly significant ($P \leq 0.005$) with $F_{4,76} = 4.08$. The period of oscillation for each "best-fitting" model is determined using the frequency, c_i, such that $2\pi/c_i$ = the period. The periods of oscillation, along with their asymptotic 95% confidence intervals, are (in months) 11.40 (9.53, 14.17); 5.11 (4.52, 5.86); and 6.64 (6.18, 7.17) for $\bar{Y}_t$, $\bar{X}_t$, and $\bar{Y}_{act}$, respectively. The asymptotic standard errors for the frequencies are 0.04690 ($\bar{Y}_t$), 0.08022 ($\bar{X}_t$) and 0.03027 ($\bar{Y}_{act}$).

DISCUSSION

Outstanding among these results is the unambiguous existence of non-random, seasonal oscillations in both the sine and cosine components of monthly mean angular orientation and the monthly mean activity of sea catfish, *Arius felis*. These cycles had significant periods of oscillation of 11.40, 5.11, and 6.64 months, respectively. These significant oscillations were exhibited by fish exposed only to the natural, local photoperiod, but otherwise maintained and monitored in a homogeneous laboratory environment. The existence of such a (seasonal) time-compensated sun compass [or, sun-orientation rhythm (Hasler and Schwassman, 1960)] is indicative of a circadian neural mechanism influencing behavior (Meirer and Fivizzani, 1980). Time-compensating sun orientation has been demonstrated for many fishes (see Quinn, 1984).

In addition, since all behavioral monitoring was conducted in constant darkness, these observed oscillations in angular orientation and activity indicate the existence of an endogenous oscillator(s) (presumably entrained by the exogenous photoperiod) which triggers non-random cycles of directional biases in monthly mean angular orientation and non-random cycles in monthly mean activity of these fish which persist for at least 24 h without reference to the entraining photoperiod. This would be of importance to the fish during migration should they swim below the photic zone, at night, or on overcast days. The distributions of orientation angles and activity of sea catfish monitored for 24 h in constant darkness have previously been shown to be not statistically different from fish similarly monitored under an LD 12:12 photoperiod approximating the local photoperiod (Steele, 1984). This persistence of the seasonal activity and orientation rhythms following removal of the environmental cue (*i.e.*, the sun) is a recognized characteristic of endogenous rhythms (*e.g.*, Schwassman, 1960).

For all three cyclical models the oscillations had annual, bimodal distributions which can be roughly correlated with the observed return migration of sea catfish to estuaries for spawning [from as early as March to as late as August (Gunter, 1947; Ward, 1957)] and their subsequent migration to offshore waters from approximately October through December (Gunter, 1947; Ward, 1957; pers. obs.). The sine ($\bar{Y}_t$) component of monthly mean orientation had a relative minima in its cycle during March and a relative maxima during September (Fig. 3). The cycle for the cosine component ($\bar{X}_t$) exhibited relative maxima during March-April and August-September. Relative minima occurred during June and November (Fig. 4). Monthly mean activity (Fig. 5) peaked during March and September-October, with minimal activity occurring during June-July (when the fish would be, presumably, in the estuaries) and December-January (when the offshore migration has presumably ended). March has been documented as the earliest month of the inshore spawning migration of sea catfish, with October through December approximately encompassing the period of offshore migration (*e.g.*, Gunter, 1947; Ward, 1957). More precise

correlation of the behavior of the experimental population with field data is not possible for a number of reasons.

Given the wide range in dates of observed migration, and the extended period during which fish were collected (July through September) it is possible that sea catfish from a number of "subgroups" making the annual inshore-offshore migration at different times during the season are represented. Such a situation may account, at least in part, for the lack of significant correlation between monthly mean activity and monthly mean vector intensity ($r_s = -0.1468$). Intuitively, these parameters should have a significant positive correlation, especially if they are related to migration. Also, the presence of fish from different spawning groups may explain the sometimes "wide" range seen in monthly individual orientation data (Figs. 2– 4). This may also be compounded by the relatively small monthly sample sizes.

Additionally, the absence in this laboratory environment of other environmental cues for triggering the migratory response and clues for its subsequent direction which the fish may normally use could also interfere with precise correlation of the observed laboratory behavior with field data. Other laboratory factors which may also inhibit the complete expression of "natural" migratory orientation and activity include the relatively confined spaces of the behavioral monitoring tank and holding tanks (thus severely limiting the fishes' progression in a "preferred" direction) and the lack of social facilitation during behavioral monitoring. Although the fish were maintained in community holding tanks, the behavioral data were collected from individuals because of design limitations of the data acquisition apparatus. Sea catfish migrate in schools (*e.g.*, Gunter, 1947; Ward, 1957). Lack of social facilitation, as well as the absence of other environmental cues and clues which may normally be used, may be especially important if the fish collected were repeat migrants, and if learning is involved in the migratory process (*e.g.*, Bitterman, 1984).

Finally, the fish were transported approximately 300 miles north of their capture site (Port Aransas, lat. 27°50.0′ N, long. 97°3.5′ W; College Station, approximate lat. 30°19.6′ N, approximate long. 96°16.5′ W). Although changes in latitude (and, therefore, the sun's altitude) alter sun-orientation responses in fishes, the displacement distances reported are considerably greater than in this study (see Hasler and Schwassman, 1960; Schwassman, 1960; Schwassman and Hasler, 1964). The fish were maintained a minimum of three months in the laboratory prior to experimentation and, therefore, exposed to the local daily photoperiod for at least this time (longer if a fish was caught at the beginning of the collecting period and/or monitored later in the following year; no individual data is available on time of capture *versus* time of monitoring). How the change in location may have affected monthly mean orientation, or whether the experience with the local photoperiod was of sufficient duration to ameliorate any such effects could not be evaluated.

However, as seen in Figure 2, the individual monthly mean orientation vectors observed in the laboratory are appropriate for fish entering and leaving the estuary system in the vicinity of Port Aransas (roughly west and east, respectively, with undoubtedly some north-south component) at the corresponding times reported for the inshore-offshore migrations (*e.g.*, Gunter, 1947; Ward, 1957). Results of Hotelling's second-order test (Hotelling, 1931; Batschelet, 1978; Table III) indicate significant clumping of the individual vectors around each monthly mean vector, except during January [Franks *et al.* (1972) have reported that sea catfish become "widely dispersed" during the winter months.] Such maintenance of appropriate seasonal orientation (and activity) by the experimental population, especially when considering the above discussion of factors which may have adversely affected an appropriate response, is considered evidence that the seasonal migrations of sea catfish must be

strongly oriented and directed in the field, and do not proceed by a simple random-walk process.

Why some fishes possess endogenous rhythmicity is not yet completely understood (Goudie *et al.*, 1983). Numerous exogenous mechanisms have been implicated in cueing both activity and orientation of fishes, including photoperiod and light intensity (*e.g.*, Richardson and McCleave, 1972; Goudie *et al.*, 1983; Steele, 1984), temperature (*e.g.*, Byrne, 1968; Goodlad *et al.*, 1974; Neill, 1984), feeding and social behavior (Goudie *et al.*, 1983), tidal and lunar cycles, and currents (*e.g.*, Saila, 1961; Arnold and Cook, 1984; Pfeiler, 1984), etc. However, the results presented here suggest that photoperiod alone can act as an exogenous mechanism for entraining an endogenous oscillator(s) in cueing (*i.e.*, triggering) seasonal oscillations in angular orientation and activity of sea catfish. Indeed, previous work (Steele, 1984) indicates the existence of at least two distinct control mechanisms governing angular orientation and locomotion of sea catfish that are light regulated (directly or indirectly) either by the length of the photoperiod (angular orientation) or by the transition from light to darkness (diel locomotor activity). This is not to say, however, that sea catfish (and other fishes) do not use additional exogenous cues in their natural habitats to "fine tune" their migratory behavior. Additionally, orientation during migration need not be confined to a single sensory modality or system of clues (Adler, 1970; Leggett, 1977). Observed migration patterns in fishes are undoubtedly the result of complex summations of many environmental forces (*e.g.*, see Clark, 1925; Walker, 1952; Gerking, 1959; Goodlad *et al.*, 1974; Matis *et al.*, 1974, 1977; Meier and Fivizzani, 1980; Barstow, 1983; Arnold and Cook, 1984; Cook, 1984; Neill, 1984). However, photoperiod alone apparently triggered non-random, seasonal oscillations in angular orientation and activity in this experimental population of sea catfish. These oscillations seen in the laboratory correspond roughly to observed migratory patterns in the species, and could be caused by an entrained endogenous mechanism controlling the cueing of migration. Several studies have demonstrated that Pacific salmon (*Oncorhynchus* spp.) also select appropriate directional headings in the absence of rheotactic, thermal, olfactory, or salinity cues (see review by Quinn, 1984). Quinn (1982) proposed that the assessment of photoperiod (daylength, or rate of change in daylength) combines with an endogenous circannual rhythm in these salmon to provide a "calendar sense." Such a mechanism could also be operating in sea catfish.

The exact nature of this (hypothesized) endogenous cueing of angular orientation and activity in migrations of sea catfish (and other fishes) remains unknown but must have an underlying physiological basis. Physiological involvement of the pineal organ in seasonal reproduction (depending on season, photoperiod and/or temperature) has been demonstrated in some fishes (*e.g.*, Fenwick, 1970; De Vlaming, 1975; De Vlaming and Vodicnik, 1978). Although relatively few studies examining seasonal changes in the pineal gland of fish have been reported (see Vivien-Roels *et al.*, 1979), there are indications of seasonal functional variations in the biochemical activity of the pineal (see Vivien-Roels, 1981), and of pineal involvement in regulating seasonal rhythms in fishes (*e.g.*, Morita, 1966; Eriksson, 1972; Kavaliers, 1980). Melatonin synthesis by the teleostean pineal gland is a well-documented nocturnal event (Gern *et al.*, 1981). It has been hypothesized that melatonin may provide a "template" to provide timing information for maintenance of entrained diel, circadian and circannual cycles (Gern *et al.*, 1981; Steele, 1984). Melatonin may act either directly or indirectly to influence biological rhythms, perhaps through the actions of serotonin, a well-known neurotransmitter, which is an intermediate in the synthesis of melatonin (Martin, 1978; Norris, 1980) and for which

non-random, seasonal oscillations in content in the pineal complex and lateral eye of lamprey, *Lampetra planeri*, has been demonstrated (Vivien-Roels and Meiniel, 1983).

From the results of this study, however, it is not possible to assert a physiological role for the pineal complex in cueing the observed non-random, seasonal oscillations in angular orientation and locomotor activity of sea catfish, nor their migratory behavior in the field. However, the results presented demonstrate that exposure of the experimental population to daily fluctuations in the natural photoperiod alone is sufficient to trigger seasonal cycles in the orientation and activity of the fish, which, combined with information in the literature (*e.g.*, Fenwick, 1970; De Vlaming, 1975; De Vlaming and Vodicnik, 1978; Gern *et al.*, 1981; Goudie *et al.*, 1983) suports such an hypothesis. Additional experimental data on the relative roles of photoperiod and other environmental factors on pineal activity and its interactions with hormones involved in the reproductive endocrinology of fishes in general (*e.g.*, Donaldson, 1973) and sea catfish in particular are needed before a complete explanation of the observations is possible.

To state that the observed maintenance of seasonally appropriate compass headings by sea catfish monitored in constant darkness is characteristic of an endogenous rhythm is not particularly instructive in understanding the mechanism involved in directing this orientation. However, the guidance mechanism of oceanic, or open-water, orientation and navigation during migration is still not understood, and a matter of considerable controversy (Leggett, 1977, 1984; Quinn, 1984; Quinn and Groot, 1984a). Many hypothetical mechanisms have been proposed, some of which are applicable to this study, while others are not. For example, the random walk hypothesis (Saila and Shappy, 1963; Leggett, 1984) appears insufficient (as discussed above) to explain the observed seasonal cycles in orientation, as are the hypothesized guidance mechanisms of bicoordinate navigation and magnetic-, electroreception (see Quinn, 1982, 1984). The confines of the behavioral arena limit the movement of fish to 210 cm in any direction. This distance is certainly insufficient for bicoordinate navigation to be operating, or to cross the necessary lines of declination required if magnetic guidance was being used (see Quinn, 1982; Leggett, 1984). Also, the double-walled steel of the monitoring tank would certainly disrupt any "normal" electromagnetic patterns. The effects of other environmental clues potentially useful in directing movement (*e.g.*, thermal, salinity, or olfactory gradients, currents, wave swell, etc.) and the influence of prior learning during migration could not be evaluated.

The underlying mechanism being used by the fish for directing the observed cycles in orientation (at least in this laboratory situation, *i.e.*, in constant darkness and the absence of environmental clues) may be time-compensating sun-compass orientation and/or inertial guidance. A number of fish species have been shown to possess a sun-compass mechanism for orientation (*e.g.*, see Hasler *et al.*, 1958, 1969; Quinn, 1984). The results of this study indicate that photoperiod entrains an endogenous oscillator to cue the observed seasonal cycles in orientation and activity. The fish may also be using the sun to maintain a preferred direction once selected. If so, the 24 h in constant darkness was insufficient to uncouple the "internal clock" of the circadian rhythm by which a sun-compass mechanism operates (Schwassman, 1960; Adler, 1970). Thus, time-compensated movements relative to the "learned" rate of change of daylength (and, therefore, the sun's position) could be used to maintain the appropriate compass heading. Inertial guidance (*i.e.*, angle compensation), for which there is some evidence in fishes, cannot, however, be ignored. Kleerekoper *et al.* (1969, 1970) provided evidence of an inertial guidance system in

the orientation of goldfish (*Carassius auratus*) monitored in a laboratory situation. Recently, Harden Jones (1984a, b) presented field data suggesting the use of inertial clues by migrating plaice (*Pleuronectes platessa*). Harden Jones hypothesized that the labyrinth could provide the basis for an inertial guidance system, especially if the selected heading could be continually corrected by reference to external clues. However, Kleerekoper *et al.* (1969, 1970) maintained that a direction of progression (orientation), once established, could be maintained by continuous compensation of turning angles in the absence of directional clues, as is the case here.

Whether either, or both, of these proposed systems of directional guidance are actually used by sea catfish to maintain a selected compass heading in this laboratory environment (or, in the field) cannot, of course, be asserted without reservation. Too little is known about the clues used for orientation and concomitant movement by this species under natural conditions. It is also unknown whether sun-compass orientation and/or inertial guidance could adequately direct orientation in sea catfish for longer than 24 h without reference to external clues. However, given the earlier discussion of proposed directing mechanisms, and the results of this study, time-compensating sun-compass orientation and/or a system of inertial guidance (angle compensation) appear to be the only appropriate mechanisms which could be directing the orientation of the fish in this situation.

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